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The strength of migratory connectivity for birds en route to breeding through the Gulf of Mexico

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The strength of migratory connectivity is a measure of the cohesion of populations among phases of the annual cycle, including breeding, migration, and wintering. Many Nearctic-Neotropical species have strong migratory connectivity between breeding and wintering phases of the annual cycle. It is less clear if this strength persists during migration when multiple endogenous and exogenous factors may decrease the cohesion of populations among routes or through time along the same routes. We sampled three bird species, American redstart *Setophaga ruticilla*, ovenbird *Seiurus aurocapilla*, and wood thrush *Hylocichla mustelina*, during spring migration through the Gulf of Mexico region to test if breeding populations differentiate spatially among migration routes or temporally along the same migration routes and the extent to which within-population timing is a function of sex, age, and carry-over from winter habitat, as measured by stable carbon isotope values in claws ($\delta^{13}C$). To make quantitative comparisons of migratory connectivity possible, we developed and used new methodology to estimate the strength of migratory connectivity (MC) from probabilistic origin assignments identified using stable hydrogen isotopes in feathers (δ^2H). We found support for spatial differentiation among routes by American redstarts and ovenbirds and temporal differentiation along routes by American redstarts. After controlling for breeding origin, the timing of American redstart migration differed among ages and sexes and ovenbird migration timing was influenced by carry-over from winter habitat. The strength of migratory connectivity did not differ among the three species, with each showing weak breeding-to-spring migration MC relative to prior assessments of breeding-wintering connectivity. Our work begins to fill an essential gap in methodology and understanding of the extent to which populations remain together during migration, information critical for a full annual cycle perspective on the population dynamics and conservation of migratory animals.

Keywords: migration, migratory connectivity, seasonal interaction

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Introduction

Migration, the regular and repeated seasonal movements of animals, is driven by complex behavioral, ecological, and evolutionary processes with profound consequences for populations and species. Migratory connectivity describes the linkages of individuals and populations between one season of the annual cycle and another that result from within-species variability in migratory behavior (Webster et al. 2002, Marra et al. 2006). The strength of migratory connectivity, more specifically, describes the extent to which populations remain cohesive between seasons. When migratory connectivity is strong, populations are cohesive through multiple seasons of the annual cycle and when migratory connectivity is weak populations that are cohesive during one season of the annual cycle disperse during other seasons (Cohen et al. 2018). The strength of migratory connectivity is fundamental to a full annual cycle perspective on population limitation and conservation because it describes the extent to which individuals remain associated between seasons and, therefore, are exposed to the same environmental conditions and selective pressures (Webster et al. 2002). The events and conditions that populations are exposed to throughout the year have consequences for individual fitness, population dynamics, and community structure (Block et al. 2005, Benson et al. 2011, Hostetler et al. 2015, Marra et al. 2015). As a result, an understanding of the strength of migratory connectivity is essential for fundamental ecology and evolution as well as for effective conservation efforts.

Technology to study the movements of migratory animals throughout the year is improving our understanding of migratory connectivity, though year-round patterns remain poorly understood for most species. Research on migratory connectivity has commonly focused on avian species (Bridge et al. 2011, Hobson et al. 2014, Ruegg et al. 2014, Rushing et al. 2014, Thorup et al. 2014, Taylor et al. 2017) but is equally relevant for migratory species of any taxonomic group (Sullivan et al. 2012, Morrison and Bolger 2014, Quillfeldt et al. 2015, Vander Zanden et al. 2015, Acevedo et al. 2017, Nishizawa et al. 2018). Among the well-studied Nearctic-Neotropical songbirds, most species have strong breeding-wintering migratory connectivity: western breeding populations winter further west in Central America while eastern breeding populations winter further east in Mexico and the Caribbean (i.e. parallel migratory connectivity; Clegg et al. 2003, Norris et al. 2006, Jones et al. 2008, Fraser et al. 2012, Drake et al. 2013, Hallworth et al. 2015, Stanley et al. 2015). Still, these studies describe patterns between stationary breeding and wintering ranges. Although stronger migratory connectivity between stationary ranges might imply differential passage routes and timing, the cohesion of populations en route has been less well studied (Bauer et al. 2016).

The consideration of the strength of migratory connectivity en route must involve spatial and temporal components because populations may segregate along different routes or they may use the same routes but at different times

(Benson et al. 2011, Bauer et al. 2016, Briedis et al. 2016, Paxton and Moore 2017). An optimal migration strategy should minimize distance, time, and predation risk and/or maximize arrival condition (Alerstam 2011). Minimizing migration distance should result in strong migratory connectivity with separate populations using non-overlapping, parallel routes. However, migration routes and timing are also influenced by exogenous factors encountered en route such as weather conditions and distributions of resources (e.g. suitable habitat; Buler et al. 2007, Cohen et al. 2017). En route migratory connectivity strength could be weakened when populations encounter variable environmental conditions and strive to maximize arrival condition or minimize time, as opposed to simply minimizing migration distance (Alerstam 2001, Hahn et al. 2014, Bayly et al. 2017, Shamoun-Baranes et al. 2017). For example, multiple lines of evidence suggest that birds will counter crosswinds to prevent drifting off course and variability in when, where, and how strongly this compensation occurs could weaken migratory connectivity (Liechti 2006, Horton et al. 2016, 2018).

Seasonal interactions also influence various aspects of migration. In particular, winter habitat is known to influence spring migration timing and energetic condition (Bearhop et al. 2004, Boone et al. 2010, González-Prieto and Hobson 2013, Paxton and Moore 2015, Graham et al. 2016). Seasonal interactions may in turn influence the strength of en route migratory connectivity by altering stopover behavior or routes used and migration speed (Bauer et al. 2016, Briedis et al. 2016, Paxton and Moore 2017). For example, American redstarts *Setophaga ruticilla* that over-winter in more xeric habitat depart later and in poorer condition for spring migration than those in more mesic habitat and this influences breeding arrival timing and condition (Marra et al. 1998, Tonra et al. 2011, McKellar et al. 2013, Cooper et al. 2015). Therefore, carry-over from winter could weaken the temporal connectivity of populations en route.

En route migratory connectivity strength is an information gap for most species and regions. Therefore, we estimated migratory connectivity for three species of long-distance Neotropical-Nearctic migratory birds, American redstart, ovenbird *Seiurus aurocapilla*, and wood thrush *Hylocichla mustelina*, as they traverse the northern coast of the Gulf of Mexico (GOM) in spring. All three of these species have some degree of differentiation between breeding and wintering ranges (Norris et al. 2006, Hallworth and Marra 2015, Hallworth et al. 2015, Stanley et al. 2015) and breeding populations of American redstarts and ovenbirds differ in spring migration passage timing through one GOM site (Langin et al. 2009). Therefore, we expected these species to maintain some spatial and temporal segregation among migration routes. However, because endogenous and exogenous factors may weaken migratory connectivity en route, we expected the strength of migratory connectivity to be weaker during migration than between breeding and winter stationary ranges. To make this comparison, we developed and used new methodology to estimate and compare the strength of

migratory connectivity from probabilistic origin assignments identified using stable hydrogen isotopes in feathers (δ2H). We further expected differences between ages and sexes and carry-over from winter habitat to influence within-population migration timing, such that older, male birds from more mesic winter habitat migrate earlier through the coast of the GOM than younger, female birds from more xeric habitat, respectively (Paxton and Moore 2015). An understanding of the spatial and temporal distribution of populations en route is critical because events encountered during migration can have cascading effects on everything from survival and reproductive success to disease transmission and timing of annual cycle events (Ahola et al. 2004, Visser et al. 2004, Tøttrup et al. 2008, 2012, Hewson et al. 2016).

Methods

Study species and sites

Migratory connectivity for American redstart, ovenbird, and wood thrush are among the best understood of Nearctic-Neotropical bird species. For all three of these species, western breeding populations predominately winter further west in Central America and Mexico while central and eastern breeding populations predominately winter in the Caribbean (American redstart and ovenbird) or further east in Central America (wood thrush) (Norris et al. 2006, Rushing et al. 2014, Hallworth et al. 2015, Stanley et al. 2015, Haché et al. 2017). Based on the strength of migratory connectivity between breeding and wintering areas (Hallworth and Marra 2015, Stanley et al. 2015, Cohen et al. 2018), we expected en route migratory connectivity to be weaker for wood thrush than for American redstart and ovenbird.

We sampled migrating birds at three stopover sites along the GOM coast, western (Texas), central (Louisiana), and eastern (Florida) (Supplementary material Appendix 1). Birds were captured with mist-nets during peak spring migration (Cohen et al. 2015) from 2012–2014 at the western and central sites and 2013–2014 at the eastern site. Sampling largely overlapped in timing, although the eastern and central sites opened slightly later in the spring than the western site. Upon capture, we collected two claws (~1.5 mm) and one tail feather (the third from the interior right) from each individual. Age (SY, second year; ASY, after second year; or AHY, after hatch year) for all species and sex for American redstart were determined based on Pyle (1997).

Isotope analysis

Stable isotope analyses of feather (δ²H) and claw (δ¹³C) samples were conducted using the methods described in Rushing et al. (2016). The latitudinal gradient of abundance of hydrogen isotopes (δ²H) in North American precipitation is incorporated into feathers grown at those latitudes (Hobson et al. 2012). The tail feathers that we collected during migration were retained throughout the year so the stable δ²H abundance reflects the geographic origin from

the previous breeding season. See Supplementary material Appendix 1 for methods used to assign migrating birds to likely breeding origin. Previous work has shown that some bird species use habitat along a moisture gradient during winter that is reflected in habitat-specific δ¹³C values in tissues such that birds with depleted δ¹³C levels in blood and claws likely grew those tissues in more mesic winter habitat (Marra et al. 1998, Bearhop et al. 2004).

Statistical analysis

We used two linear models to test hypotheses about spatial (model 1) and temporal (model 2) en route migratory connectivity of breeding birds passing through the northern coast of the GOM during spring. To account for uncertainty in breeding latitude we generated 1000 estimates of breeding latitude for each individual by drawing a random value from a normal distribution with mean equal to that individual's estimated breeding latitude and standard deviation calculated from the standard error of the estimated latitude. The estimated latitudes were then used as either the response (model 1) or the predictor (model 2) variable in the models described below. For each regression coefficient, we report the mean and the lower (2.5%) and upper (97.5%) confidence interval (CI) of the 1000 bootstrap estimates and judged continuous predictors as significant when the confidence intervals did not overlap zero and levels of a factor different when the confidence intervals did not overlap.

We tested for differences in the breeding latitudes of individuals passing through the GOM at different locations using a linear regression model. In the following description, subscript i refers to individual, r to route (western, central, eastern), and t to year (2012–2014):

$$\text{Lat}_{i,r,t} = \alpha_{1,r} + \xi_{1,t} + \varepsilon_{i,t}$$

where $\text{Lat}_{i,r,t}$ is the breeding latitude of individual i, as estimated from the δ²H value, $\alpha_{1,r}$ is the predicted breeding latitude for birds passing through route r, $\xi_{1,t}$ is a random year effect to control for annual variation in breeding latitude among all routes, and $\varepsilon_{i,t}$ is a normally distributed error term.

We used a second regression model to test for differences in the timing of individuals passing through the GOM as a function of breeding latitude, route, age, sex, and winter habitat (δ¹³C):

$$\text{DOY}_{i,r,t} = \alpha_{2,r} + \xi_{2,t} + \beta_1 \text{Lat}_i + \beta_{2,r} \text{Lat}_i + \beta_3 I(\text{age}_i) + \beta_4 I(\text{sex}_i) + \beta_5 \delta^{13}C_i + \beta_{6,a} \delta^{13}C_i + \beta_{7,s} \delta^{13}C_i + \varepsilon_{i,t}$$

where $\text{DOY}_{i,r,t}$ is the day of the year (1 January = 1) that individual i migrated through the GOM along route r in year t, $\alpha_{2,r}$ is the mean passage days of after second year females on route r, β_1 is the mean effect of breeding latitude across all routes, $\beta_{2,r}$ is the difference between the mean effect of latitude and the effect of latitude along route r, β_3 is the effect of age, $I(\text{age}_i)$ is a dummy variable indicating whether an individual was a second year bird, β_4 is the effect of sex, $I(\text{sex}_i)$

is a dummy variable indicating whether an individual was a male, β_5 is the effect of winter habitat across all individuals, $\beta_{6,a}$ is the difference between the effect of winter habitat between second year and after second year, $\beta_{7,s}$ is the difference between the effect of winter habitat between males and females, and $\xi_{2,t}$ and $\mathcal{E}_{i,t}$ are the same as in model 1. Positive values of β_1 indicate that individuals from southern latitudes pass through the GOM earlier than individuals from higher latitudes and positive values of β_5 indicate that individuals from more mesic habitat, with lower, more depleted $\delta^{13}C$ values, migrate earlier. Sex and its interaction with winter habitat quality were only included in models for American redstart. Two American redstarts were not included in this analysis due to missing age and sex data. For birds with either missing $\delta^{13}C$ values or values above −20 and below −24 (likely outliers resulting from analytical errors; Marra et al. 1998), we used the mean $\delta^{13}C$ value (n = 18, 17, 12 for American redstarts, ovenbirds, and wood thrush, respectively). The two numeric predictor variables, latitude and winter habitat, were not strongly correlated (all r < 0.15).

We assessed support for the influence of the six main effects and three interaction terms in the passage timing model using Akaike's information criterion corrected for small sample sizes (AICc). We fit a global model and all possible subset models, ranked by ΔAICc (dredge function in R package MuMIn; Barton 2018). Because we also needed to account for uncertainty in breeding latitude for each individual during model selection, we repeated this procedure 1000 times, each time randomly generating an estimated breeding latitude for each individual using the method described above. For each model, we report the mean AICc weight and mean ΔAICc from the 1000 bootstraps.

To compare the strength of migratory connectivity across studies, we developed new methodology to estimate the strength of migratory connectivity (MC) from probabilistic assignment of breeding latitude using stable hydrogen isotope values in feathers (δ^2H). The MigConnectivity R package was developed to estimate MC incorporating uneven sampling among regions and uncertainty associated with the data type used to measure transition probabilities of populations between one season and another (MigConnectivity 0.3.0; Hostetler and Hallworth 2017). Here we extended the estMC function to include uncertainty associated with transition probabilities estimated from isotope assignment and use simulation to test for its accuracy. Similar to the approach for light-level geolocator data (Cohen et al. 2018), we used a bootstrap, sampling with replacement from the animals with isotope data. In this case, location uncertainty was applied by sampling from probabilistic isotope assignments using a multinomial distribution to generate random points for each sampled animal (Supplementary material Appendix 1). We used species-specific capture rates at each site as a measure of relative abundance and measured MC between spring stopover sites and breeding latitudes represented by isotope bands equivalent to 12‰ (the standard deviation used to generate probabilistic isotope-assignments, Supplementary material Appendix 1).

We developed a new function, diffMC, within the MigConnectivity R package to test for differences among independent estimates of MC. It does this by sampling with replacement from each species' own samples (bootstrap or otherwise) of MC, then taking the difference:

$$\Delta MC_{ij}^{*s} = MC_i^{*s} - MC_j^{*s}$$

where ΔMC_{ij}^{*s} is the sth sampled difference in MC between species i and j and MC_i^{*s} is the sth sampled MC value for species i. The difference in migratory connectivity strength between the two species $\left(\Delta MC_{ij} \right)$ and its confidence interval can be estimated by the mean and bias-corrected quantiles of the sampled differences (Supplementary material Appendix 1).

Results

We captured and sampled American redstarts (n = 97), ovenbirds (n = 150), and wood thrush (n = 184) on three spring migration routes through the coast of the GOM (Table 1). The day of spring that the species passed through the sites (25th to 75th percentiles) was similar for American redstarts (17 April to 8 May) and ovenbirds (20 April to 2 May) but earlier and over a shorter time period for wood thrush (16 April to 23 April). Within our samples, American redstarts were predominately older (< 40% SY), wood thrush were predominately younger (> 60% SY), and ovenbirds were evenly mixed (50% SY), although 35 and 26% ovenbird and wood thrush were not aged, respectively (Table 1).

Based on isotopic assignments, American redstarts migrating further west through the GOM bred further north ($\alpha_{1,W}$ = 46.84° [LCI = 46.20, UCI = 47.52], $\alpha_{1,C}$ = 41.04° [40.55, 41.51], $\alpha_{1,E}$ = 39.02° [38.04, 39.99]; Fig. 1A). Ovenbirds migrating through the western and central GOM bred further north ($\alpha_{1,W}$ = 47.31° [46.73, 47.88], $\alpha_{1,C}$ = 46.66° [46.14, 47.22]) than those migrating through the eastern GOM ($\alpha_{1,E}$ = 44.65° [43.73, 45.58]; Fig. 1B). Wood thrush breeding populations did not differentiate among routes by breeding latitude ($\alpha_{1,W}$ = 38.08° [37.45, 38.68], $\alpha_{1,C}$ = 37.90° [37.45, 38.37], $\alpha_{1,E}$ = 38.03° [36.90, 39.27]; Fig. 1C).

We evaluated differences in the timing of migration by breeding latitude as well as by route, year, age, sex, and carryover from winter habitat. The models with the most explanatory power (mean ΔAICc < 2) for the timing of spring migration passage included breeding latitude for American redstart and wood thrush, but not ovenbird (Table 2). Southern breeding American redstarts migrated earlier than northern breeding individuals (Fig. 2), with birds breeding 0.88° further north each day of spring migration (β_1 = 0. 88° d⁻¹ [0. 84, 0.91], Fig. 3). Despite inclusion in top supported models, the effects of latitude on wood thrush migration was not significant (β_1 = 0.19° d⁻¹ [−0.67, 1.01]). However, the top supported model for wood thrush also included the interaction term between route and breeding latitude, with southern breeding birds migrating earlier than northern through the central, but not the western or eastern routes (Fig. 3).

Table 1. Mean (SE) estimated breeding latitude and day of year for migration route, year, age and sex.

Species	Parameter		Breeding latitude	Day of year [a]	n
American redstart	Route	western	46.05 (1.37)	121.0 (1.6)	39
		central	41.37 (1.45)	111.4 (1.7)	42
		eastern	40.00 (1.79)	116.8 (2.2)	16
	Year	2012	42.59 (1.74)	115.2 (2.3)	30
		2013	40.98 (1.65)	118.5 (2.2)	28
		2014	44.83 (1.38)	115.2 (1.6)	39
	Age[b]	ASY	42.06 (1.08)	113.4 (1.4)	67
		SY	45.42 (1.74)	122.6 (1.4)	28
	Sex[c]	female	40.31 (1.52)	118.3 (1.7)	32
		male	44.51 (1.12)	115.3 (1.5)	64
Ovenbird	Route	western	48.21 (0.57)	116.5 (0.9)	67
		central	47.91 (0.56)	115.3 (1.2)	63
		eastern	46.06 (0.75)	114.1 (1.5)	20
	Year	2012	46.94 (0.65)	116.1 (1.6)	36
		2013	47.10 (0.59)	117.4 (1.1)	41
		2014	48.61 (0.57)	114.5 (1.0)	73
	Age	ASY	48.15 (0.66)	113.8 (1.0)	49
		SY	47.64 (0.60)	118.2 (1.1)	49
		AHY	47.62 (0.62)	115.1 (1.3)	52
Wood thrush	Route	western	37.98 (0.11)	111.4 (1.0)	68
		central	37.94 (0.08)	105.8 (0.8)	106
		eastern	38.25 (0.31)	110.0 (0.9)	10
	Year	2012	37.94 (0.14)	105.5 (1.2)	49
		2013	37.57 (0.11)	112.1 (1.4)	44
		2014	38.19 (0.08)	107.5 (0.8)	91
	Age	ASY	37.72 (0.14)	105.3 (1.6)	38
		SY	38.12 (0.09)	108.8 (0.8)	99
		AHY	37.86 (0.13)	108.7 (1.2)	47

[a] Day of year, 90 = 31 March.
[b] SY = second year, young birds on first spring migration, ASY = after second year, any age after the first spring migration, AHY = after hatch year, individuals that could not be classified as either SY or ASY. There were only two AHY American redstarts and they were excluded from analyses.
[c] It was only possible to identify sex for American redstart. There was only one unknown sex and it was excluded from analyses.

The top models for all three species supported difference among routes and years on the timing of spring migration passage (Table 2). For American redstarts, passage timing was earlier through the central GOM ($\alpha_{2,C}$ = 79.8 DOY [78.2, 81.2]) and did not differ between the western ($\alpha_{2,W}$ = 83.6 DOY [81.9, 85.3]) and eastern ($\alpha_{2,E}$ = 86.4 DOY [84.7, 88.0]) routes. The same pattern was true for wood thrush, with earlier passage through the central GOM ($\alpha_{2,C}$ = 52.6 DOY [25.2, 79.4]) and no difference between the western ($\alpha_{2,W}$ = 101.4 DOY [68.9, 134.7]) and eastern ($\alpha_{2,E}$ = 120.6 DOY [81.9, 155.7]) routes. In contrast, ovenbird passage timing did not differ among routes ($\alpha_{2,W}$ = 153.8 DOY [120.7, 186.8], $\alpha_{2,C}$ = 153.1 DOY [119.7, 186.6], $\alpha_{2,E}$ = 149.9 DOY [116.9, 183.0]). Passage timing was earlier during 2014 for
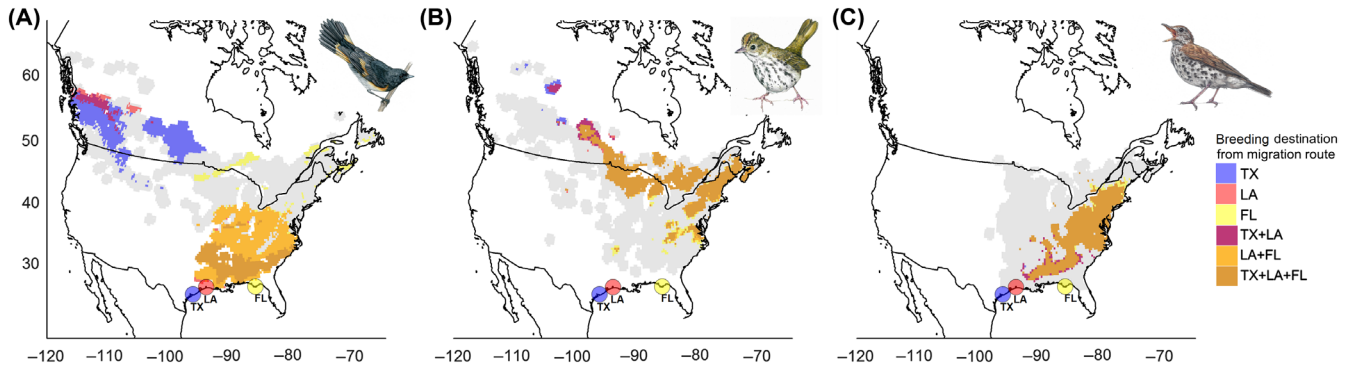

Figure 1. Probable origins (75th percentile) to breeding range (light gray) of American redstart (A), ovenbird (B), and wood thrush (C) captured at stopover sites during spring migration through the western (Texas), central (Louisiana), and eastern (Florida) coast of the Gulf of Mexico. Bird images by Lauren Dibiccari.

Table 2. Relative support for the influence of six main effects (latitude, passage route, year, age, sex and $\delta^{13}C$) and three interaction terms (route by latitude, age by $\delta^{13}C$, sex by $\delta^{13}C$) on the timing of spring migration passage through the Gulf of Mexico using Akaike's information criterion corrected for small sample sizes (AICc). Latitude is the estimated breeding latitude assignment of young and old (age) migrating birds moving through the western, central, and eastern (route) coast of the Gulf of Mexico during 2012–2014 (year). The $\delta^{13}C$ values of tissues are signatures of winter habitat (see text). Only models for American redstart included sex and sex by $\delta^{13}C$. We incorporate error in breeding latitude assignment into model selection and report the mean and error of weights and ΔAICc from 1000 bootstraps of 100 individuals. Parameters in the models with the most explanatory power (ΔAICc < 2.0) were assessed for the significance of their explanatory variables.

Species	Model[a]	df	mean w_i	sd w_i	mean ΔAICc
American redstart	**latitude, route, year, sex, age**	**9**	**0.345**	**0.035**	**0.00**
	latitude, route, year, sex, age, $\delta^{13}C$	10	0.120	0.014	2.11
	latitude, route, year, sex	8	0.114	0.036	2.32
	latitude, route, year, sex, age, latitude:route	11	0.092	0.027	2.71
	latitude, route, year, sex, $\delta^{13}C$, age:$\delta^{13}C$	9	0.035	0.004	4.57
	latitude, route, year, sex, $\delta^{13}C$	11	0.035	0.011	4.71
	latitude, route, year, sex, age, $\delta^{13}C$, sex:$\delta^{13}C$	11	0.034	0.004	4.62
	latitude, route, year, sex, latitude:route	10	0.034	0.013	4.79
	latitude, route, year, sex, age, $\delta^{13}C$, latitude:route	12	0.030	0.009	4.95
Ovenbird	**route, year, age, $\delta^{13}C$**	**9**	**0.355**	**0.045**	**0.00**
	year, age, $\delta^{13}C$	**7**	**0.163**	**0.028**	**1.57**
	route, year, age	8	0.097	0.022	2.63
	latitude, route, year, age, $\delta^{13}C$	10	0.076	0.009	3.07
	latitude, year, age, $\delta^{13}C$	8	0.062	0.014	3.53
	route, year, age, $\delta^{13}C$, age:$\delta^{13}C$	11	0.045	0.008	4.15
	year, age	6	0.034	0.009	4.76
Wood thrush	**latitude, route, year, latitude:route**	**9**	**0.231**	**0.147**	**1.15**
	latitude, route, year	**7**	**0.223**	**0.126**	**1.40**
	latitude, route, year, $\delta^{13}C$, latitude:route	10	0.088	0.060	3.11
	latitude, route, year, $\delta^{13}C$	8	0.085	0.047	3.31
	latitude, route, year, age	9	0.071	0.043	3.68
	latitude, route, year, age, latitude:route	11	0.065	0.046	3.68

[a] Top supported models, ΔAICc $\leq$ 5, for each species included.

American redstart ($\xi_{2,2013} = 1.0$ DOY [2.9, 1.6], $\xi_{2,2014} = -4.4$ DOY [–5.1, –3.8]) and ovenbird ($\xi_{2,2013} = 1.7$ DOY [1.4, 2.1], $\xi_{2,2014} = -1.1$ DOY [–1.4, –0.7]) and later during 2013 for wood thrush ($\xi_{2,2013} = 4.6$ DOY [3.8, 5.5], $\xi_{2,2014} = 0.4$ DOY [–0.5, 1.2]).

Top supported models for the timing of spring migration passage included age and sex for American redstarts and age and winter habitat ($\delta^{13}C$) for ovenbirds, while neither age nor winter habitat were supported for wood thrush (Table 2). Among American redstarts, males migrated five days earlier than females ($\beta_4 = -5.3$ DOY [–5.9, –4.8]) and older birds migrated three to four days earlier than younger birds on their first spring migration ($\beta_3 = -3.5$ DOY [–4.0, –2.9]; Fig. 4A). Older ovenbirds migrated four to five days
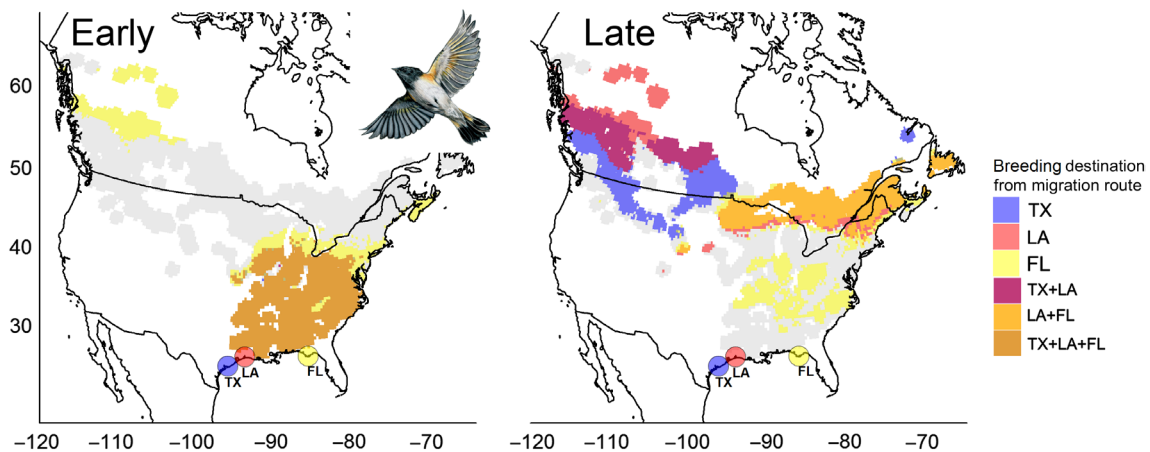

Figure 2. Probable origins (75th percentile) to breeding range (light gray) of American redstart during the first (Early) and second (Late) half of spring migration through the western (Texas), central (Louisiana), and eastern (Florida) coast of the Gulf of Mexico. Bird image by Lauren Dibiccari.
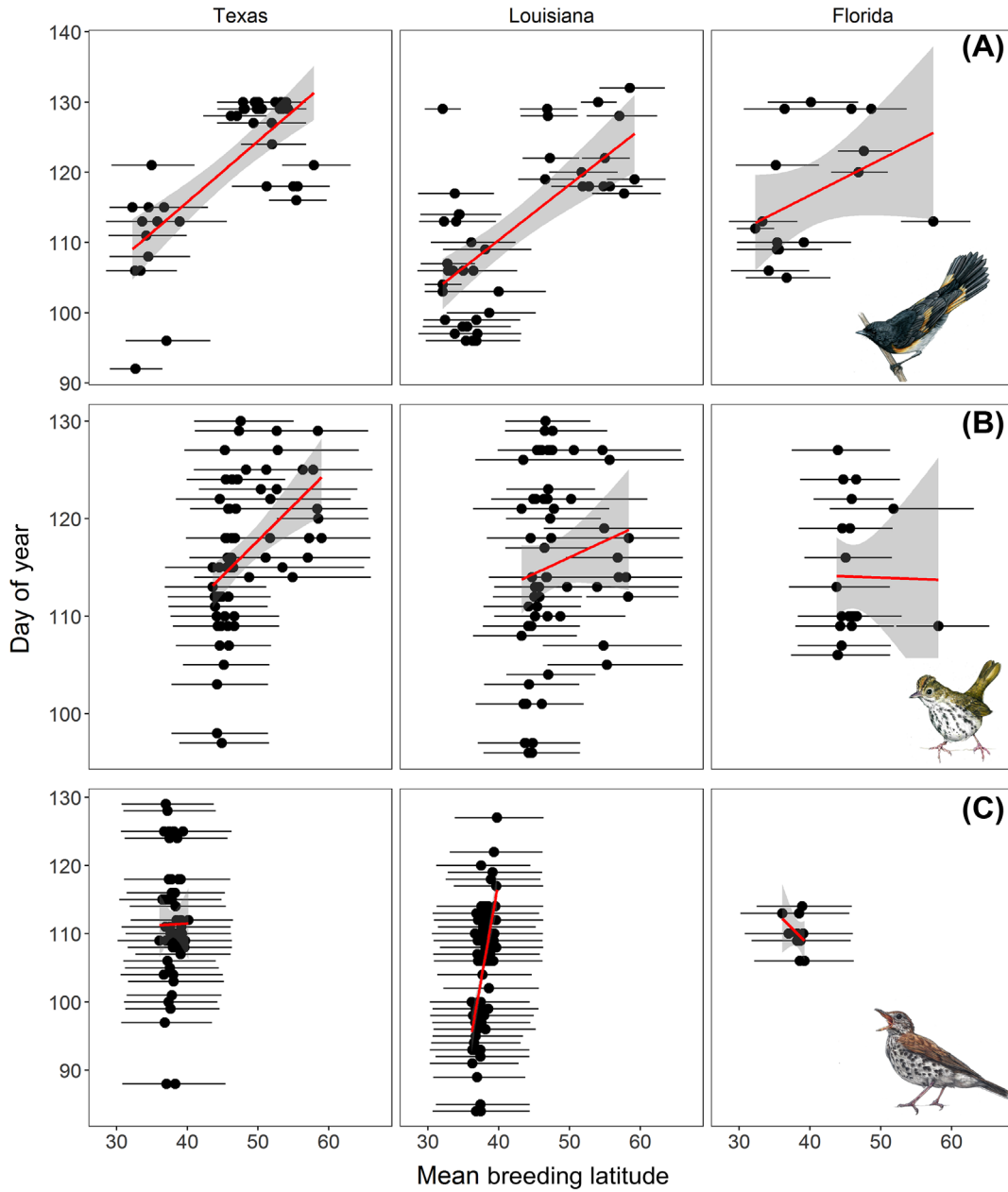
Figure 3. Migration passage timing (day of year, 90 = 31 March) for (A) American redstart, (B) ovenbird, and (C) wood thrush through the western (Texas), central (Louisiana), and eastern (Florida) coast of the Gulf of Mexico by breeding latitude. The ribbons are CI from a standard regression and the black lines are error around each latitude estimate.

earlier than younger birds on their first spring migration ($\beta_3 = -4.7$ DOY [−5.0, −4.4]; Fig. 4B). Stable carbon isotope values from tissues of American redstarts (mean = −22.52 [min = −24.80, max = −20.09], n = 79), ovenbirds (−23.18 [−25.36, −20.71], n = 133) and wood thrush (−23.64 [−24.98, −20.72], n = 172) reflected those collected from wet forested and dry scrub over-wintering habitats (Marra et al. 1998) but only ovenbird migration timing was influenced by winter habitat. Ovenbirds with more depleted $\delta^{13}C$ values, indicative of more mesic winter habitat, migrated earlier than those with less depleted values, indicative of more xeric

habitat, ($\beta_5 = 1.6$ d ppm $\delta^{13}C^{-1}$ [1.4, 1.7]). Because sampling dates were uneven, we also ran analyses excluding data when all sites were not open and found similar results with one exception, without the first week of data there were no differences in timing between male and female American redstarts.

MC was weaker en route (American redstart 0.04 [LCI = 0.007, UCI = 0.12], ovenbird 0.04 [−0.004, 0.10], wood thrush 0.01 [−0.08, 0.16]), as compared to values reported for breeding to wintering and MC values were not different from zero for ovenbird and wood thrush. While simulations indicated a small bias in MC estimated from
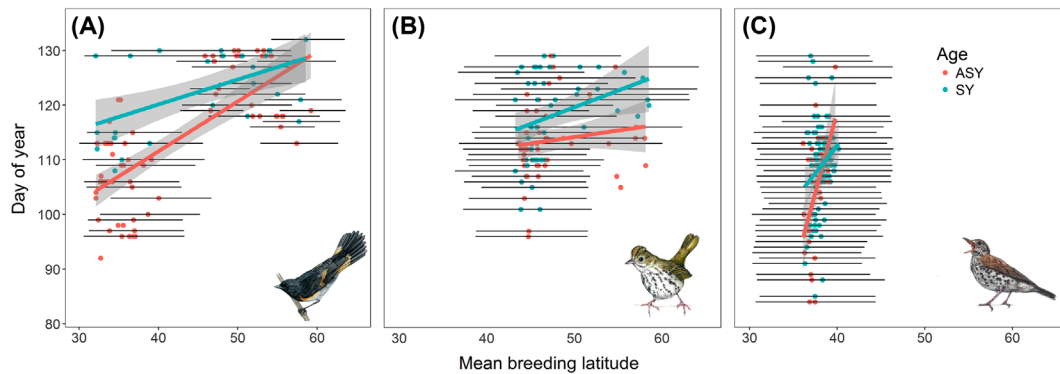
Figure 4. Migration passage timing (day of year, 90 = 31 March) for (A) American redstart, (B) ovenbird, and (C) wood thrush during their first (SY = second year) or subsequent spring migrations (ASY = after second year). The ribbons are CI from a standard regression and the black lines are error around each latitude estimate.

isotopes, coverage of the true value was high (98.5%; true MC included in the 95% credible interval; Supplementary material Appendix 1). There was no significant difference in MC among the three species through the GOM (American redstart and ovenbird ΔMC = –0.005 [LCI = –0.07, UCI = 0.08], American redstart and wood thrush ΔMC = 0.03 [–0.12, 0.13], ovenbird and wood thrush ΔMC = 0.003 [–0.12, 0.13]. For American redstarts, the species for which spring migration passage timing varied by breeding latitude, MC was stronger during the second half of the season (early 0.06 [–0.004, 0.36], late 0.08 [0.002, 0.30], Fig. 2).

Discussion

We found support for weak en route migratory connectivity and species-specific differences in timing among ages and sexes and due to carry-over from winter habitat. Species with strong breeding-winter migratory connectivity all had weak breeding-spring migration migratory connectivity while maintaining some segregation en route. Although American redstarts have yet to be tracked during migration through the GOM, limited tracking data for the other two species supports these results. For instance, ovenbirds breeding in western Canada were tracked through Texas and Louisiana to Central America, while those breeding in the eastern U.S. took an eastern route through Florida to winter in the Caribbean (Hallworth et al. 2015). And though wood thrush tracked across the GOM exhibited considerable annual variability in migration routes (Stanley et al. 2012), spring passage longitude through the GOM region was positively correlated with breeding longitude (Stanley et al. 2015). Therefore, it is possible that wood thrush also maintain some strong parallel migratory connectivity en route which we did not find due to the limited resolution of our stable isotope data. These analyses did not allow us to accurately measure probable breeding longitude and the narrower latitudinal extent of the wood thrush breeding range may have limited our ability to detect population-specific routes and timing for this species. Nevertheless, our data support the idea that

while local adaptation may lead to strong breeding-wintering migratory connectivity, variable and unpredictable environmental conditions may lead to weak migration-breeding migratory connectivity. Therefore, navigating the shortest distance migration route may be less beneficial than minimizing energetic cost and risk of mortality (Alerstam 2001, Hahn et al. 2014, Shamoun-Baranes et al. 2017), potentially weakening migratory connectivity en route as compared to during stationary phases of the annual cycle. Meanwhile, reorientation toward specific breeding or wintering areas near the destination would maintain strong migratory connectivity and is supported by the benefits of site fidelity during stationary phases of the annual cycle (Karlsson et al. 2010).

We found support for a diffuse migration strategy with weaker MC strength en route (all < 0.05) as compared to published MC values between breeding and wintering for ovenbird (0.61 ± 0.10) and a related measure that does not incorporate uncertainty, r_M (Mantel correlation; Cohen et al. 2018), for ovenbird (0.84; Hallworth and Marra 2015) and wood thrush (0.33; Stanley et al. 2012). More work is needed to understand the factors that influence the strength of migratory connectivity among migratory species and throughout the annual cycle (Finch et al. 2017) and the use of a standardized quantitative measure incorporating uncertainly across data types will increasingly make comparisons possible (Cohen et al. 2018). While quantitative comparisons of MC across species and seasons may be influenced by geographic differences in ranges and regions, simulations suggest that MC is only slightly biased low by incorrect delineation of populations into regions (Cohen et al. 2018). Our work begins to fill an essential gap of understanding how populations of some species are distributed during migratory phases of the annual cycle.

We found support for a temporal component to migratory connectivity strength with southern breeding populations migrating earlier along the same routes than northern breeding populations. However, this pattern was strongest for American redstarts, occurring through all three routes, and was weak for wood thrush, with temporal differentiation only through the central route. An earlier study at a single

site on the central GOM, found that southern populations migrated earlier than northern for four out of five species (hooded warblers *Wilsonia citrina*; American redstarts; black-and-white warblers *Mniotilta varia*; and ovenbirds; but not northern waterthrushes *Seiurus noveboracensis*; Langin et al. 2009). These results support a temporal component to en route migratory connectivity strength but no other study has included multiple routes around this region. It is further possible that these populations differ in winter latitude such that migration passage timing is related to migration distance (i.e. leap-frog migration). Nevertheless, we found individuals from across the latitudinal extent of the breeding ranges passed through sites around the GOM but breeding latitudes were synchronous through all or some sites, depending on the species (Bauer et al. 2016). More information, including connections to wintering areas and breeding arrival timing, is needed to understand why temporal population synchrony occurs along some migration routes but not others. Information about the temporal distributions of populations en route is key to untangling many aspects of migration biology including the role of resource phenology in shaping migration passage timing, stopover strategies, and the temporal organization of the annual cycle (Finch et al. 2014, Bauer et al. 2016, Briedis et al. 2016, Paxton and Moore 2017).

After controlling for breeding latitude, male American redstarts migrated before females, older American redstarts and ovenbirds migrate before younger, and ovenbirds from more mesic habitat migrate earlier than those from more xeric habitat. Birds may migrate earlier as a function of increased experience with migration, access to better resources during winter, or stronger motivation to secure high-quality breeding territories and mates (Marra et al. 1998, Morbey and Ydenberg 2001, Stewart et al. 2002). Males and females should not differ in experience during spring migration and may be under similar time pressure during spring because both benefit from increased reproductive performance with early breeding arrival (Smith and Moore 2005, Cooper et al. 2009). Alternatively, the time schedule for females may be adjusted to reduce overlap with males during migration passage, if they are socially subordinate (Moore et al. 2003). It is also possible that males migrate earlier because they occupy higher quality habitats on wintering grounds and, thus, depart earlier because they are in better condition for spring migration (Marra et al. 1998). Young birds on their first spring migration may be delayed as a result of dominance by older birds on the wintering grounds (Marra et al. 1993, 1998) or they may not benefit from arriving early when competition for territories with older birds may be greater (Stewart et al. 2002, Cooper et al. 2009). Interestingly, older American redstarts were considerably earlier than younger conspecifics during the first part of the spring, when southern breeding populations are migrating, but the difference was minimal later in the spring, when northern breeding populations are migrating (Fig. 4A). Further, when we excluded the first week of data, before the eastern site was open, we did not find

a difference in timing between male and female American redstarts. This suggests that, for northern breeding populations, differences in the speed of spring migration among ages and sexes may become more pronounced within continental North America, after crossing the GOM (Cohen et al. 2015).

Carry-over to spring migration from winter habitat is not universal for species or populations (Pedersen et al. 2016, Briedis et al. 2018), even within the Nearctic-Neotropical system (González-Prieto and Hobson 2013, McKinnon et al. 2015). The influence of winter habitat on spring migration is likely a function of the strength of migratory connectivity to wintering areas that differ in environmental conditions and/or differential use of habitats that differ in quality (Marra et al. 1998, Wilson et al. 2011, Cresswell 2014). We found evidence of winter environment influencing migration timing for ovenbirds. For wood thrush, this result is supported by individual tracking data (McKinnon et al. 2015). Surprisingly, we did not find a carry-over effect of winter habitat on migration timing for American redstarts, a relationship that has support for winter departure and breeding arrival (Marra et al. 1998, Tonra et al. 2011, Cooper et al. 2015). This discrepancy is likely due to a lack of power in our study, with many American redstarts lacking winter habitat data, particularly for the eastern route (56% individuals missing winter habitat data). Carry-over effects from winter habitat on migration timing may be both species- and population-specific and best measured throughout the annual cycle (Briedis et al. 2018) and migration routes across a region. For example, it is possible that we missed breeding populations that do not migrate through the GOM region (e.g. eastern breeding ovenbirds migrating through eastern Florida; Haché et al. 2017) or pass over coastal areas and stopover further inland (Buler et al. 2017, Gómez et al. 2017). Comparison among populations along all possible migration routes would not be trivial to accomplish but is likely to elucidate further patterns to the strength of migratory connectivity, including carry-over from winter.

A growing body of migratory connectivity research has focused on the connections between breeding and wintering seasons. Following smaller animals remains challenging, yet understanding MC during migration is equally important to understanding the dynamics of migratory populations. It has not yet been possible to quantitatively compare MC among multiple phases of the annual cycle (Cohen et al. 2018). If en route migratory connectivity was strong, we would expect some degree of fidelity to routes, however there is little evidence that individual songbirds use the same stopover sites between years (Catry et al. 2004). Experienced migrants likely have the ability to navigate to previously visited stopover sites (Akesson et al. 2014), but minimizing time and energetic costs in unfavorable weather, avoiding predation, and finding suitable stopover habitat may outweigh the benefits of maintaining the shortest distance route (Catry et al. 2004, Moore 2018). Further, changes in the availability of suitable stopover habitat along routes would likely select for longer and fewer stopovers than en route philopatry. As technology

advances, finer-scale spatial and temporal data will increase our ability to accurately estimate how migratory connectivity strength changes throughout the annual cycle.

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Supplementary material (Appendix ECOG-03974 at <www.ecography.org/appendix/ecog-03974>). Appendix 1.